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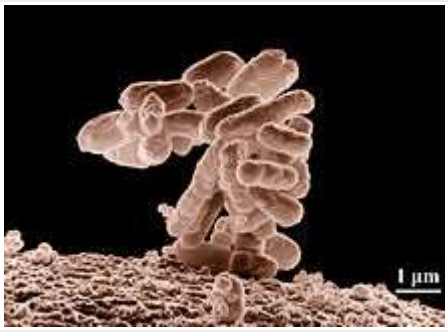
Escherichia coli

Escherichia coli (/ˌɛʃəˈrɪkiə ˈkoʊlaɪ/),[1][2] also known as ***E. coli*** (/ˌiː ˈkoʊlaɪ/),[2] is a Gram-negative, facultative anaerobic, rod-shaped, coliform bacterium of the genus *Escherichia* that is commonly found in the lower intestine of warm-blooded organisms (endotherms).[3][4] Most *E. coli* strains are harmless, but some serotypes (EPEC, ETEC etc.) can cause serious food poisoning in their hosts, and are occasionally responsible for food contamination incidents that prompt product recalls.[5][6] The harmless strains are part of the normal microbiota of the gut, and can benefit their hosts by producing vitamin K_2,[7] (which helps blood to clot) and preventing colonisation of the intestine with pathogenic bacteria, having a symbiotic relationship.[8][9] *E. coli* is expelled into the environment within fecal matter. The bacterium grows massively in fresh fecal matter under aerobic conditions for 3 days, but its numbers decline slowly afterwards.[10]

E. coli and other facultative anaerobes constitute about 0.1% of gut microbiota,[11] and fecal–oral transmission is the major route through which pathogenic strains of the bacterium cause disease. Cells are able to survive outside the body for a limited amount of time, which makes them potential indicator organisms to test environmental samples for fecal contamination.[12][13] A growing body of research, though, has examined environmentally persistent *E. coli* which can survive for many days and grow outside a host.[14]

The bacterium can be grown and cultured easily and inexpensively in a laboratory setting, and has been intensively investigated for over 60 years. *E. coli* is a chemoheterotroph whose chemically defined medium must include a source of carbon and energy.[15] *E. coli* is the most widely studied prokaryotic model organism, and an important species in the fields of biotechnology and microbiology, where it has served as the host organism for the majority of work with recombinant DNA. Under favorable conditions, it takes as little as 20 minutes to reproduce.[16]

Escherichia coli



Scientific classification

Domain:	Bacteria
Phylum:	Proteobacteria
Class:	Gammaproteobacteria
Order:	Enterobacterales
Family:	Enterobacteriaceae
Genus:	*Escherichia*
Species:	***E. coli***

Binomial name

Escherichia coli

(Migula 1895)

Castellani and Chalmers 1919

Synonyms

- *Bacillus coli communis*

  Escherich 1885

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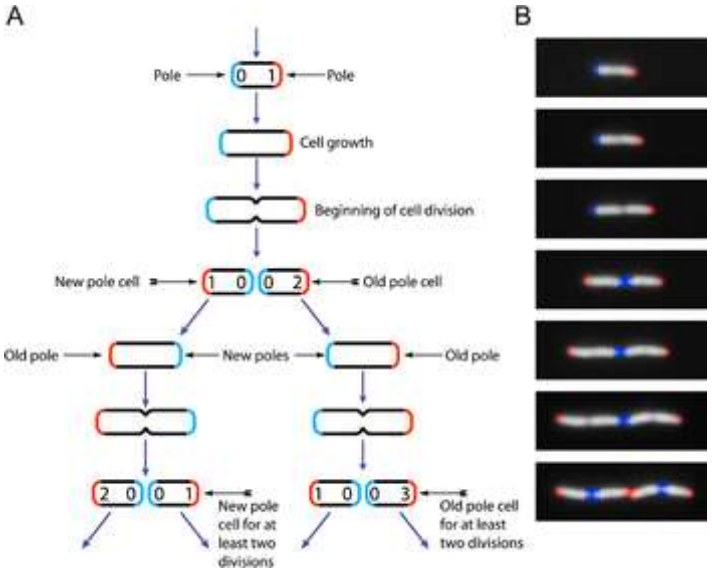
Biology and biochemistry

Type and morphology

E. coli is a Gram-negative, facultative anaerobe (that makes ATP by aerobic respiration if oxygen is present, but is capable of switching to fermentation or anaerobic respiration if oxygen is absent) and nonsporulating bacterium.[17] Cells are typically rod-shaped, and are about 2.0 μm long and 0.25–1.0 μm in diameter, with a cell volume of 0.6–0.7 μm^3.[18][19][20]

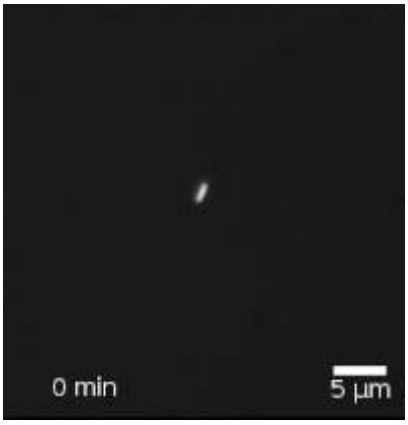
E. coli stains Gram-negative because its cell wall is composed of a thin peptidoglycan layer and an outer membrane. During the staining process, *E. coli* picks up the color of the counterstain safranin



Model of successive binary fission in *E. coli*

and stains pink. The outer membrane surrounding the cell wall provides a barrier to certain antibiotics such that *E. coli* is not damaged by penicillin.[15]

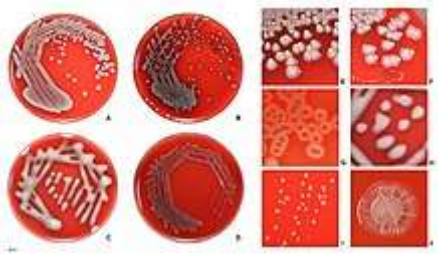
Strains that possess flagella are motile. The flagella have a peritrichous arrangement.[21] It also attaches and effaces to the microvilli of the intestines via an adhesion molecule known as intimin.[22]



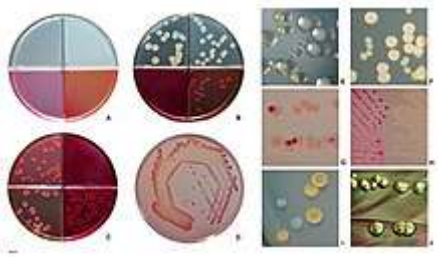
A colony of *E. coli* growing

Metabolism

E. coli can live on a wide variety of substrates and uses mixed acid fermentation in anaerobic conditions, producing lactate, succinate, ethanol, acetate, and carbon dioxide. Since many pathways in mixed-acid fermentation produce hydrogen gas, these pathways require the levels of hydrogen to be low, as is the case when *E. coli* lives together with hydrogen-consuming organisms, such as methanogens or sulphate-reducing bacteria.[23]


E. coli on sheep blood agar.

In addition, *E. coli*'s metabolism can be rewired to solely use CO_2 as the source of carbon for biomass production. In other words, this obligate heterotroph's metabolism can be altered to display autotrophic capabilities by heterologously expressing carbon fixation genes as well as formate dehydrogenase and conducting laboratory evolution experiments. This may be done by using formate to reduce electron carriers and supply the ATP required in anabolic pathways inside of these synthetic autotrophs.[24]


E. coli growing on basic cultivation media.

Culture growth

Optimum growth of *E. coli* occurs at 37 °C (98.6 °F), but some laboratory strains can multiply at temperatures up to 49 °C (120 °F).[25] *E. coli* grows in a variety of defined laboratory media, such as lysogeny broth, or any medium that contains glucose, ammonium phosphate monobasic, sodium chloride, magnesium sulfate, potassium phosphate dibasic, and water. Growth can be driven by aerobic or anaerobic respiration, using a large variety of redox pairs, including the oxidation of pyruvic acid, formic acid, hydrogen, and amino acids, and the reduction of substrates such as oxygen, nitrate, fumarate, dimethyl sulfoxide, and trimethylamine N-oxide.[26] *E. coli* is classified as a facultative anaerobe. It uses oxygen when it is present and available. It can, however, continue to grow in the absence of oxygen using fermentation or anaerobic respiration. The ability to continue growing in the absence of oxygen is an advantage to bacteria because their survival is increased in environments where water predominates.[15]

Cell cycle

The bacterial cell cycle is divided into three stages. The B period occurs between the completion of cell division and the beginning of DNA replication. The C period encompasses the time it takes to replicate the chromosomal DNA. The D period refers to the stage between the conclusion of DNA replication and the end of cell division.[27] The doubling rate of *E. coli* is higher when more nutrients are available.

However, the length of the C and D periods do not change, even when the doubling time becomes less than the sum of the C and D periods. At the fastest growth rates, replication begins before the previous round of replication has completed, resulting in multiple replication forks along the DNA and overlapping cell cycles.[28]

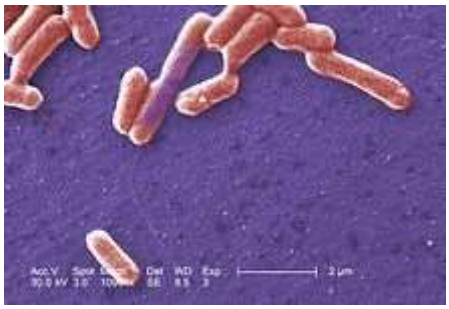
The number of replication forks in fast growing *E. coli* typically follows 2n (n = 1, 2 or 3). This only happens if replication is initiated simultaneously from all origins of replications, and is referred to as synchronous replication. However, not all cells in a culture replicate synchronously. In this case cells do not have multiples of two replication forks. Replication initiation is then referred to being asynchronous.[29] However, asynchrony can be caused by mutations to for instance DnaA[29] or DnaA initiator-associating protein DiaA.[30]

Genetic adaptation

E. coli and related bacteria possess the ability to transfer DNA via bacterial conjugation or transduction, which allows genetic material to spread horizontally through an existing population. The process of transduction, which uses the bacterial virus called a bacteriophage,[31] is where the spread of the gene encoding for the Shiga toxin from the *Shigella* bacteria to *E. coli* helped produce *E. coli* O157:H7, the Shiga toxin-producing strain of *E. coli*.

Diversity

E. coli encompasses an enormous population of bacteria that exhibit a very high degree of both genetic and phenotypic diversity. Genome sequencing of many isolates of *E. coli* and related bacteria shows that a taxonomic reclassification would be desirable. However, this has not been done, largely due to its medical importance,[32] and *E. coli* remains one of the most diverse bacterial species: only 20% of the genes in a typical *E. coli* genome is shared among all strains.[33]



Scanning electron micrograph of an *E. coli* colony.

In fact, from the more constructive point of view, the members of genus *Shigella* (*S. dysenteriae*, *S. flexneri*, *S. boydii*, and *S. sonnei*) should be classified as *E. coli* strains, a phenomenon termed taxa in disguise.[34] Similarly, other strains of *E. coli* (e.g. the K-12 strain commonly used in recombinant DNA work) are sufficiently different that they would merit reclassification.

A strain is a subgroup within the species that has unique characteristics that distinguish it from other strains. These differences are often detectable only at the molecular level; however, they may result in changes to the physiology or lifecycle of the bacterium. For example, a strain may gain pathogenic capacity, the ability to use a unique carbon source, the ability to take upon a particular ecological niche, or the ability to resist antimicrobial agents. Different strains of *E. coli* are often host-specific, making it possible to determine the source of fecal contamination in environmental samples.[12][13] For example, knowing which *E. coli* strains are present in a water sample allows researchers to make assumptions about whether the contamination originated from a human, another mammal, or a bird.

Serotypes

A common subdivision system of *E. coli*, but not based on evolutionary relatedness, is by serotype, which is based on major surface antigens (O antigen: part of lipopolysaccharide layer; H: flagellin; K antigen: capsule), e.g. O157:H7).[35] It is, however, common to cite only the serogroup, i.e. the O-antigen. At present, about 190 serogroups are known.[36] The common laboratory strain has a mutation that prevents the formation of an O-antigen and is thus not typeable.

Genome plasticity and evolution

Like all lifeforms, new strains of *E. coli* evolve through the natural biological processes of mutation, gene duplication, and horizontal gene transfer; in particular, 18% of the genome of the laboratory strain MG1655 was horizontally acquired since the divergence from *Salmonella*.[37] *E. coli* K-12 and *E. coli* B strains are the most frequently used varieties for laboratory purposes. Some strains develop traits that can be harmful to a host animal. These virulent strains typically cause a bout of diarrhea that is often self-limiting in healthy adults but is frequently lethal to children in the developing world.[38] More virulent strains, such as O157:H7, cause serious illness or death in the elderly, the very young, or the immunocompromised.[38][39]

The genera *Escherichia* and *Salmonella* diverged around 102 million years ago (credibility interval: 57–176 mya), which coincides with the divergence of their hosts: the former being found in mammals and the latter in birds and reptiles.[40] This was followed by a split of an *Escherichia* ancestor into five species (*E. albertii*, *E. coli*, *E. fergusonii*, *E. hermannii*, and *E. vulneris*). The last *E. coli* ancestor split between 20 and 30 million years ago.[41]

The long-term evolution experiments using *E. coli*, begun by Richard Lenski in 1988, have allowed direct observation of genome evolution over more than 65,000 generations in the laboratory.[42] For instance, *E. coli* typically do not have the ability to grow aerobically with citrate as a carbon source, which is used as a diagnostic criterion with which to differentiate *E. coli* from other, closely, related bacteria such as *Salmonella*. In this experiment, one population of *E. coli* unexpectedly evolved the ability to aerobically metabolize citrate, a major evolutionary shift with some hallmarks of microbial speciation.

In the microbial world, a relationship of predation can be established similar to that observed in the animal world. Considered, it has been seen that E. coli is the prey of multiple generalist predators, such as *Myxococcus xanthus*. In this predator-prey relationship, a parallel evolution of both species is observed through genomic and phenotypic modifications, in the case of E. coli the modifications are modified in two aspects involved in their virulence such as mucoid production (excessive production of exoplasmic acid alginate) and the suppression of the OmpT gene, producing in future generations a better adaptation of one of the species that is counteracted by the evolution of the other, following a co-evolutionary model demonstrated by the Red Queen hypothesis.[43]

Neotype strain

E. coli is the type species of the genus (*Escherichia*) and in turn *Escherichia* is the type genus of the family Enterobacteriaceae, where the family name does not stem from the genus *Enterobacter* + "i" (sic.) + "aceae", but from "enterobacterium" + "aceae" (enterobacterium being not a genus, but an alternative trivial name to enteric bacterium).[44][45][46]

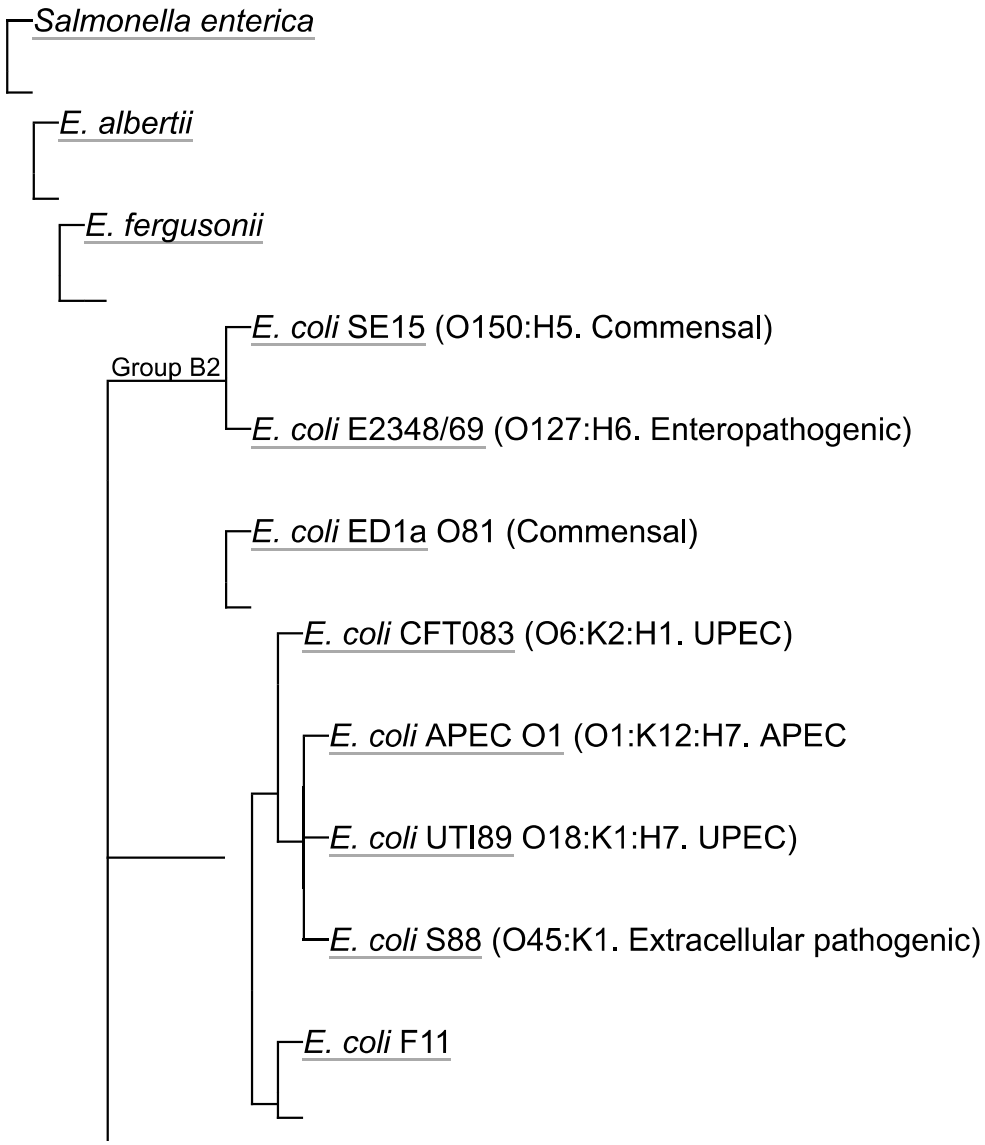
The original strain described by Escherich is believed to be lost, consequently a new type strain (neotype) was chosen as a representative: the neotype strain is U5/41^{T},[47] also known under the deposit names DSM 30083,[48] ATCC 11775,[49] and NCTC 9001,[50] which is pathogenic to chickens and has an

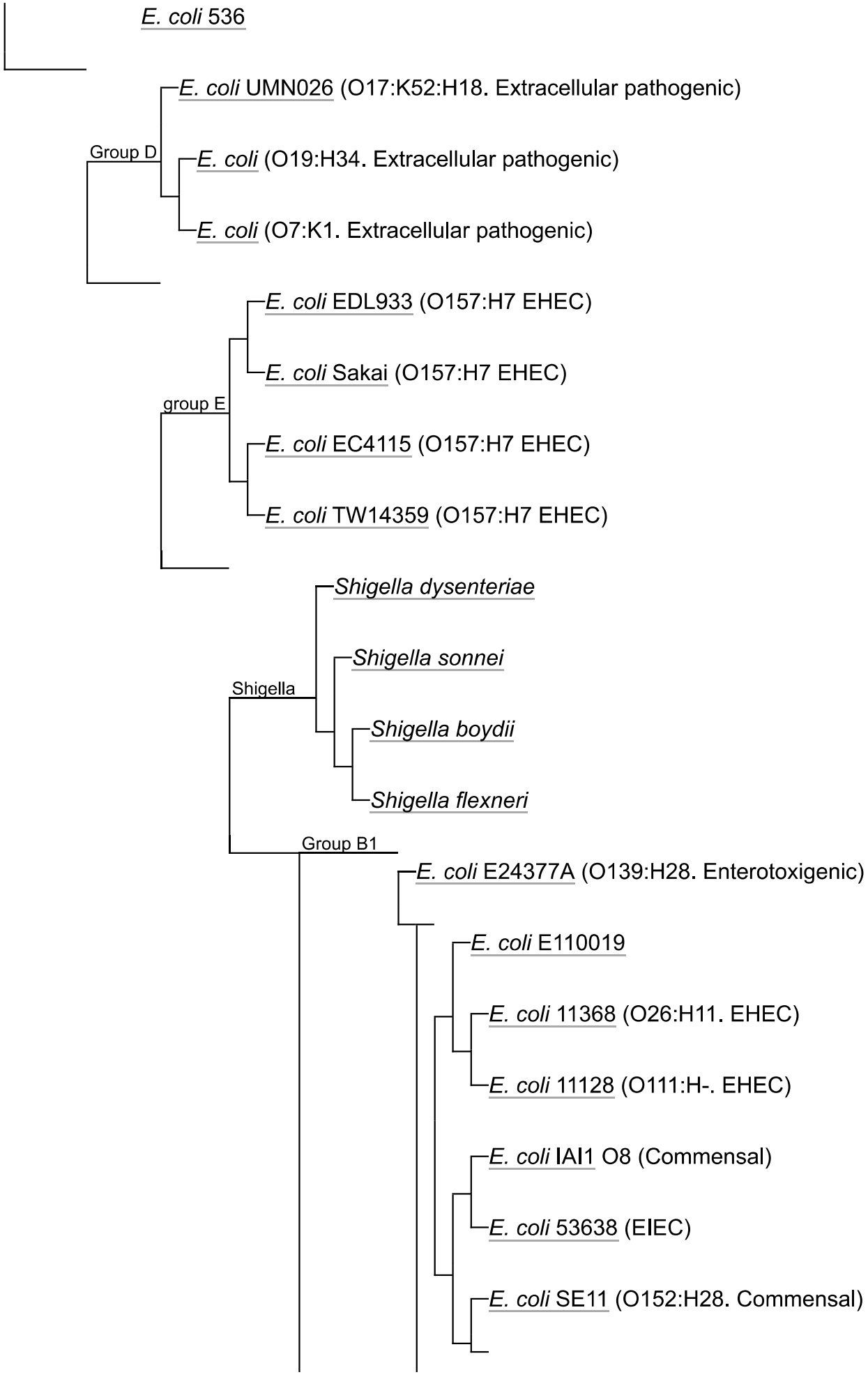
O1:K1:H7 serotype.[51] However, in most studies, either O157:H7, K-12 MG1655, or K-12 W3110 were used as a representative *E. coli*. The genome of the type strain has only lately been sequenced.[47]

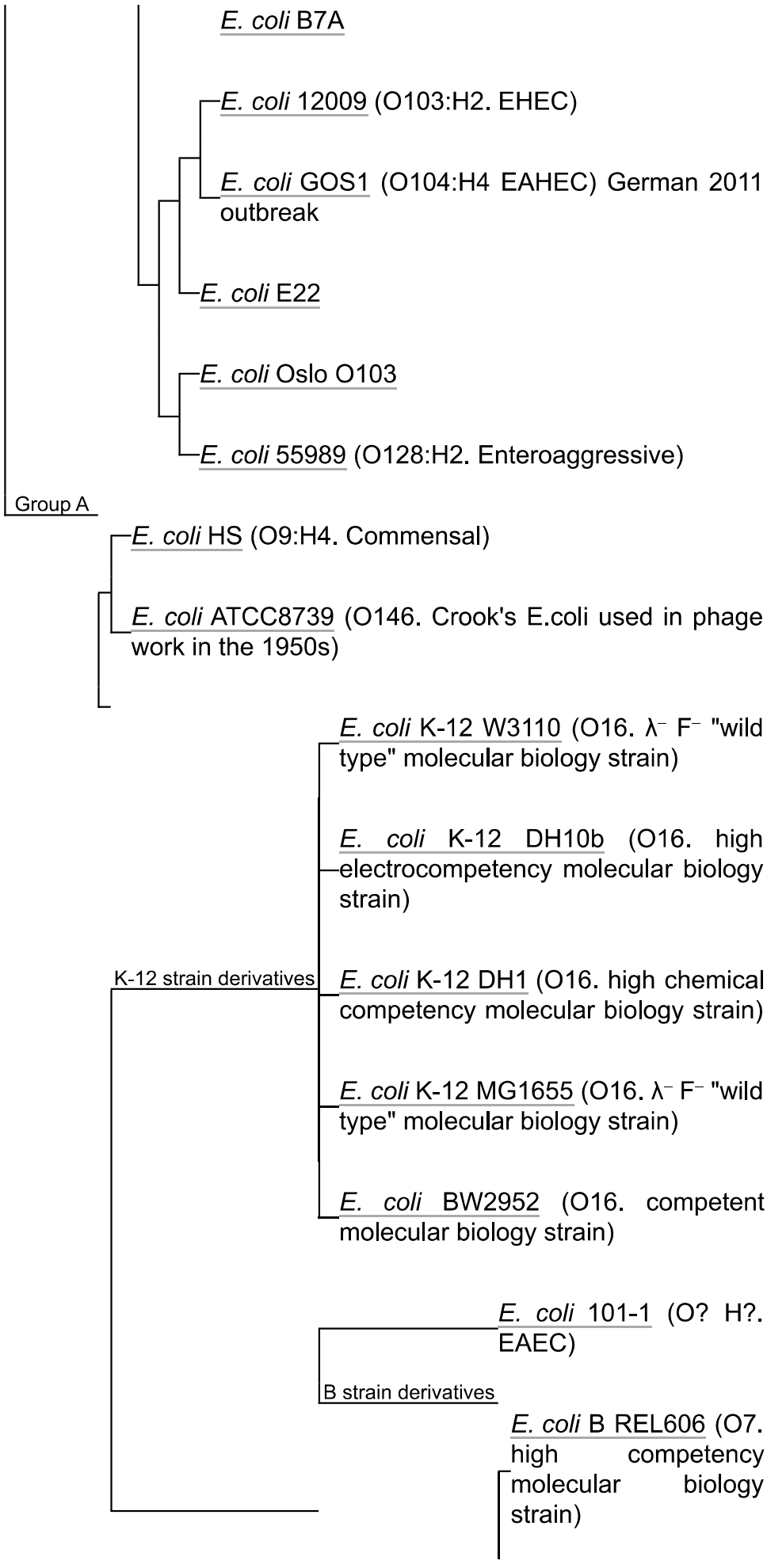
Phylogeny of *E. coli* strains

Many strains belonging to this species have been isolated and characterised. In addition to serotype (*vide supra*), they can be classified according to their phylogeny, i.e. the inferred evolutionary history, as shown below where the species is divided into six groups.[52][53] Particularly the use of whole genome sequences yields highly supported phylogenies. Based on such data, five subspecies of *E. coli* were distinguished.[47]

The link between phylogenetic distance ("relatedness") and pathology is small,[47] *e.g.* the O157:H7 serotype strains, which form a clade ("an exclusive group")—group E below—are all enterohaemorragic strains (EHEC), but not all EHEC strains are closely related. In fact, four different species of *Shigella* are nested among *E. coli* strains (*vide supra*), while *E. albertii* and *E. fergusonii* are outside this group. Indeed, all *Shigella* species were placed within a single subspecies of *E. coli* in a phylogenomic study that included the type strain,[47] and for this reason an according reclassification is difficult. All commonly used research strains of *E. coli* belong to group A and are derived mainly from Clifton's K-12 strain (λ^+ F^+; O16) and to a lesser degree from d'Herelle's *Bacillus coli* strain (B strain)(O7).

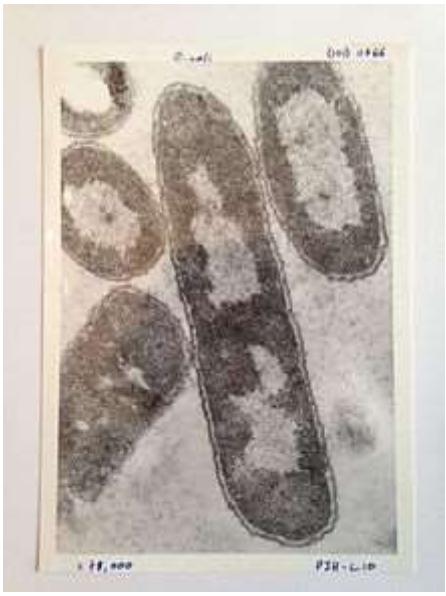



E. coli 536
E. coli UMN026 (O17:K52:H18. Extracellular pathogenic)
Group D
E. coli (O19:H34. Extracellular pathogenic)
E. coli (O7:K1. Extracellular pathogenic)
E. coli EDL933 (O157:H7 EHEC)
E. coli Sakai (O157:H7 EHEC)
group E
E. coli EC4115 (O157:H7 EHEC)
E. coli TW14359 (O157:H7 EHEC)
Shigella dysenteriae
Shigella sonnei
Shigella
Shigella boydii
Shigella flexneri
Group B1
E. coli E24377A (O139:H28. Enterotoxigenic)
E. coli E110019
E. coli 11368 (O26:H11. EHEC)
E. coli 11128 (O111:H-. EHEC)
E. coli IAI1 O8 (Commensal)
E. coli 53638 (EIEC)
E. coli SE11 (O152:H28. Commensal)


E. coli B7A
E. coli 12009 (O103:H2. EHEC)
E. coli GOS1 (O104:H4 EAHEC) German 2011 outbreak
E. coli E22
E. coli Oslo O103
E. coli 55989 (O128:H2. Enteroaggressive)
Group A
E. coli HS (O9:H4. Commensal)
E. coli ATCC8739 (O146. Crook's E.coli used in phage work in the 1950s)
E. coli K-12 W3110 (O16. λ⁻ F⁻ "wild type" molecular biology strain)
E. coli K-12 DH10b (O16. high electrocompetency molecular biology strain)
K-12 strain derivatives
E. coli K-12 DH1 (O16. high chemical competency molecular biology strain)
E. coli K-12 MG1655 (O16. λ⁻ F⁻ "wild type" molecular biology strain)
E. coli BW2952 (O16. competent molecular biology strain)
E. coli 101-1 (O? H?. EAEC)
B strain derivatives
E. coli B REL606 (O7. high competency molecular biology strain)

└*E. coli* BL21-DE3 (O7. expression molecular biology strain with T7 polymerase for pET system)

Genomics



An image of *E. coli* using early electron microscopy.

The first complete DNA sequence of an *E. coli* genome (laboratory strain K-12 derivative MG1655) was published in 1997. It is a circular DNA molecule 4.6 million base pairs in length, containing 4288 annotated protein-coding genes (organized into 2584 operons), seven ribosomal RNA (rRNA) operons, and 86 transfer RNA (tRNA) genes. Despite having been the subject of intensive genetic analysis for about 40 years, many of these genes were previously unknown. The coding density was found to be very high, with a mean distance between genes of only 118 base pairs. The genome was observed to contain a significant number of transposable genetic elements, repeat elements, cryptic prophages, and bacteriophage remnants.[54]

More than three hundred complete genomic sequences of *Escherichia* and *Shigella* species are known. The genome sequence of the type strain of *E. coli* was added to this collection before 2014.[47] Comparison of these sequences shows a remarkable amount of diversity; only about 20% of each genome represents sequences present in every one of the isolates, while around 80% of each genome can vary among isolates.[33] Each individual genome contains between 4,000 and 5,500 genes, but the total number of different genes among all of the sequenced *E. coli* strains (the pangenome) exceeds 16,000. This very large variety of component genes has been interpreted to mean that two-thirds of the *E. coli* pangenome originated in other species and arrived through the process of horizontal gene transfer.[55]

Gene nomenclature

Genes in *E. coli* are usually named by 4-letter acronyms that derive from their function (when known) and italicized. For instance, *recA* is named after its role in homologous recombination plus the letter A. Functionally related genes are named *recB*, *recC*, *recD* etc. The proteins are named by uppercase acronyms, e.g. RecA, RecB, etc. When the genome of *E. coli* was sequenced, all genes were numbered (more or less) in their order on the genome and abbreviated by b numbers, such as b2819 (= *recD*). The "b" names were created after Fred Blattner, who led the genome sequence effort.[54] Another numbering system was introduced with the sequence of another *E. coli* strain, W3110, which was sequenced in Japan and hence uses numbers starting by JW... (Japanese W3110), e.g. JW2787 (= *recD*).[56] Hence, *recD* = b2819 = JW2787. Note, however, that most databases have their own numbering system, e.g. the EcoGene database[57] uses EG10826 for *recD*. Finally, ECK numbers are specifically used for alleles in the MG1655 strain of *E. coli* K-12.[57] Complete lists of genes and their synonyms can be obtained from databases such as EcoGene or Uniprot.

Proteomics

Proteome

Several studies have investigated the proteome of *E. coli*. By 2006, 1,627 (38%) of the 4,237 open reading frames (ORFs) had been identified experimentally.[58] The 4,639,221–base pair sequence of Escherichia coli K-12 is presented. Of 4288 protein-coding genes annotated, 38 percent have no attributed function. Comparison with five other sequenced microbes reveals ubiquitous as well as narrowly distributed gene families; many families of similar genes within *E. coli* are also evident. The largest family of paralogous proteins contains 80 ABC transporters. The genome as a whole is strikingly organized with respect to the local direction of replication; guanines, oligonucleotides possibly related to replication and recombination, and most genes are so oriented. The genome also contains insertion sequence (IS) elements, phage remnants, and many other patches of unusual composition indicating genome plasticity through horizontal transfer.[54]

Interactome

The interactome of *E. coli* has been studied by affinity purification and mass spectrometry (AP/MS) and by analyzing the binary interactions among its proteins.

Protein complexes. A 2006 study purified 4,339 proteins from cultures of strain K-12 and found interacting partners for 2,667 proteins, many of which had unknown functions at the time.[59] A 2009 study found 5,993 interactions between proteins of the same *E. coli* strain, though these data showed little overlap with those of the 2006 publication.[60]

Binary interactions. Rajagopala *et al.* (2014) have carried out systematic yeast two-hybrid screens with most *E. coli* proteins, and found a total of 2,234 protein-protein interactions.[61] This study also integrated genetic interactions and protein structures and mapped 458 interactions within 227 protein complexes.

Normal microbiota

E. coli belongs to a group of bacteria informally known as coliforms that are found in the gastrointestinal tract of warm-blooded animals.[44] *E. coli* normally colonizes an infant's gastrointestinal tract within 40 hours of birth, arriving with food or water or from the individuals handling the child. In the bowel, *E. coli* adheres to the mucus of the large intestine. It is the primary facultative anaerobe of the human gastrointestinal tract.[62] (Facultative anaerobes are organisms that can grow in either the presence or absence of oxygen.) As long as these bacteria do not acquire genetic elements encoding for virulence factors, they remain benign commensals.[63]

Therapeutic use

Nonpathogenic *E. coli* strain Nissle 1917, (Mutaflor) and *E. coli* O83:K24:H31 (Colinfant)[64][65]) are used as probiotic agents in medicine, mainly for the treatment of various gastrointestinal diseases,[66] including inflammatory bowel disease.[67]

Role in disease

Most *E. coli* strains do not cause disease, naturally living in the gut,[68] but virulent strains can cause gastroenteritis, urinary tract infections, neonatal meningitis, hemorrhagic colitis, and Crohn's disease. Common signs and symptoms include severe abdominal cramps, diarrhea, hemorrhagic colitis, vomiting, and sometimes fever. In rarer cases, virulent strains are also responsible for bowel necrosis (tissue death) and perforation without progressing to hemolytic-uremic syndrome, peritonitis, mastitis, sepsis, and Gram-negative pneumonia. Very young children are more susceptible to develop severe illness, such as hemolytic uremic syndrome; however, healthy individuals of all ages are at risk to the severe consequences that may arise as a result of being infected with *E. coli*.[62][69][70][71]

Some strains of *E. coli*, for example O157:H7, can produce Shiga toxin (classified as a bioterrorism agent). The Shiga toxin causes inflammatory responses in target cells of the gut, leaving behind lesions which result in the bloody diarrhea that is a symptom of a Shiga toxin-producing *E. coli* (STEC) infection. This toxin further causes premature destruction of the red blood cells, which then clog the body's filtering system, the kidneys, in some rare cases (usually in children and the elderly) causing hemolytic-uremic syndrome (HUS), which may lead to kidney failure and even death. Signs of hemolytic uremic syndrome include decreased frequency of urination, lethargy, and paleness of cheeks and inside the lower eyelids. In 25% of HUS patients, complications of nervous system occur, which in turn causes strokes. In addition, this strain causes the buildup of fluid (since the kidneys do not work), leading to edema around the lungs and legs and arms. This increase in fluid buildup especially around the lungs impedes the functioning of the heart, causing an increase in blood pressure.[72][22][73][74][75][70][71]

Uropathogenic *E. coli* (UPEC) is one of the main causes of urinary tract infections.[76] It is part of the normal microbiota in the gut and can be introduced in many ways. In particular for females, the direction of wiping after defecation (wiping back to front) can lead to fecal contamination of the urogenital orifices. Anal intercourse can also introduce this bacterium into the male urethra, and in switching from anal to vaginal intercourse, the male can also introduce UPEC to the female urogenital system.

Enterotoxigenic *E. coli* (ETEC) is the most common cause of traveler's diarrhea, with as many as 840 million cases worldwide in developing countries each year. The bacteria, typically transmitted through contaminated food or drinking water, adheres to the intestinal lining, where it secretes either of two types of enterotoxins, leading to watery diarrhea. The rate and severity of infections are higher among children under the age of five, including as many as 380,000 deaths annually.[77]

In May 2011, one *E. coli* strain, O104:H4, was the subject of a bacterial outbreak that began in Germany. Certain strains of *E. coli* are a major cause of foodborne illness. The outbreak started when several people in Germany were infected with enterohemorrhagic *E. coli* (EHEC) bacteria, leading to hemolytic-uremic syndrome (HUS), a medical emergency that requires urgent treatment. The outbreak did not only concern Germany, but also 15 other countries, including regions in North America.[78] On 30 June 2011, the German *Bundesinstitut für Risikobewertung (BfR)* (Federal Institute for Risk Assessment, a federal institute within the German Federal Ministry of Food, Agriculture and Consumer Protection) announced that seeds of fenugreek from Egypt were likely the cause of the EHEC outbreak.[79]

Incubation period

The time between ingesting the STEC bacteria and feeling sick is called the "incubation period". The incubation period is usually 3–4 days after the exposure, but may be as short as 1 day or as long as 10 days. The symptoms often begin slowly with mild belly pain or non-bloody diarrhea that worsens over several days. HUS, if it occurs, develops an average 7 days after the first symptoms, when the diarrhea is improving.[80]

Treatment

The mainstay of treatment is the assessment of dehydration and replacement of fluid and electrolytes. Administration of antibiotics has been shown to shorten the course of illness and duration of excretion of enterotoxigenic *E. coli* (ETEC) in adults in endemic areas and in traveller's diarrhea, though the rate of resistance to commonly used antibiotics is increasing and they are generally not recommended.[81] The antibiotic used depends upon susceptibility patterns in the particular geographical region. Currently, the antibiotics of choice are fluoroquinolones or azithromycin, with an emerging role for rifaximin. Oral rifaximin, a semisynthetic rifamycin derivative, is an effective and well-tolerated antibacterial for the management of adults with non-invasive traveller's diarrhea. Rifaximin was significantly more effective than placebo and no less effective than ciprofloxacin in reducing the duration of diarrhea. While rifaximin is effective in patients with *E. coli*-predominant traveller's diarrhea, it appears ineffective in patients infected with inflammatory or invasive enteropathogens.[82]

Prevention

ETEC is the type of *E. coli* that most vaccine development efforts are focused on. Antibodies against the LT and major CFs of ETEC provide protection against LT-producing, ETEC-expressing homologous CFs. Oral inactivated vaccines consisting of toxin antigen and whole cells, i.e. the licensed recombinant cholera B subunit (rCTB)-WC cholera vaccine Dukoral, have been developed. There are currently no licensed vaccines for ETEC, though several are in various stages of development.[83] In different trials, the rCTB-WC cholera vaccine provided high (85–100%) short-term protection. An oral ETEC vaccine candidate consisting of rCTB and formalin inactivated *E. coli* bacteria expressing major CFs has been shown in clinical trials to be safe, immunogenic, and effective against severe diarrhoea in American travelers but not against ETEC diarrhoea in young children in Egypt. A modified ETEC vaccine consisting of recombinant *E. coli* strains over-expressing the major CFs and a more LT-like hybrid toxoid called LCTBA, are undergoing clinical testing.[84] [85]

Other proven prevention methods for *E. coli* transmission include handwashing and improved sanitation and drinking water, as transmission occurs through fecal contamination of food and water supplies. Additionally, thoroughly cooking meat and avoiding consumption of raw, unpasteurized beverages, such as juices and milk are other proven methods for preventing *E.coli*. Lastly, avoid cross-contamination of utensils and work spaces when preparing food.[86]

Model organism in life science research

Because of its long history of laboratory culture and ease of manipulation, *E. coli* plays an important role in modern biological engineering and industrial microbiology.[87] The work of Stanley Norman Cohen and Herbert Boyer in *E. coli*, using plasmids and restriction enzymes to create recombinant DNA, became a foundation of biotechnology.[88]

E. coli is a very versatile host for the production of heterologous proteins,[89] and various protein expression systems have been developed which allow the production of recombinant proteins in *E. coli*. Researchers can introduce genes into the microbes using plasmids which permit high level expression of protein, and such protein may be mass-produced in industrial fermentation processes. One of the first useful applications of recombinant DNA technology was the manipulation of *E. coli* to produce human insulin.[90]

Many proteins previously thought difficult or impossible to be expressed in *E. coli* in folded form have been successfully expressed in *E. coli*. For example, proteins with multiple disulphide bonds may be produced in the periplasmic space or in the cytoplasm of mutants rendered sufficiently oxidizing to allow disulphide-bonds to form,[91] while proteins requiring post-translational modification such as glycosylation for stability or function have been expressed using the N-linked glycosylation system of *Campylobacter jejuni* engineered into *E. coli*.[92][93][94]

Modified *E. coli* cells have been used in vaccine development, bioremediation, production of biofuels,[95] lighting, and production of immobilised enzymes.[89][96]

Strain K-12 is a mutant form of *E. coli* that over-expresses the enzyme Alkaline Phosphatase (ALP).[97] The mutation arises due to a defect in the gene that constantly codes for the enzyme. A gene that is producing a product without any inhibition is said to have constitutive activity. This particular mutant form is used to isolate and purify the aforementioned enzyme.[97]

Strain OP50 of *Escherichia coli* is used for maintenance of *Caenorhabditis elegans* cultures.

Strain JM109 is a mutant form of *E. coli* that is recA and endA deficient. The strain can be utilized for blue/white screening when the cells carry the fertility factor episome[98] Lack of recA decreases the possibility of unwanted restriction of the DNA of interest and lack of endA inhibit plasmid DNA decomposition. Thus, JM109 is useful for cloning and expression systems.

Model organism

E. coli is frequently used as a model organism in microbiology studies. Cultivated strains (e.g. *E. coli* K12) are well-adapted to the laboratory environment, and, unlike wild-type strains, have lost their ability to thrive in the intestine. Many laboratory strains lose their ability to form biofilms.[99][100] These features protect wild-type strains from antibodies and other chemical attacks, but require a large expenditure of energy and material resources. *E. coli* is often used as a representative microorganism in the research of novel water treatment and sterilisation methods, including photocatalysis. By standard plate count methods, following sequential dilutions, and growth on agar gel plates, the concentration of viable organisms or CFUs (Colony Forming Units), in a known volume of treated water can be evaluated, allowing the comparative assessment of materials performance.[101]

In 1946, Joshua Lederberg and Edward Tatum first described the phenomenon known as bacterial conjugation using *E. coli* as a model bacterium,[102] and it remains the primary model to study conjugation.[103] *E. coli* was an integral part of the first experiments to understand phage genetics,[104] and early researchers, such as Seymour Benzer, used *E. coli* and phage T4 to understand the topography of gene structure.[105] Prior to Benzer's research, it was not known whether the gene was a linear structure, or if it had a branching pattern.[106]

E. coli was one of the first organisms to have its genome sequenced; the complete genome of *E. coli* K12 was published by *Science* in 1997[54]

From 2002 to 2010, a team at the Hungarian Academy of Science created a strain of *Escherichia coli* called MDS42, which is now sold by Scarab Genomics of Madison, WI under the name of "Clean Genome. E.coli",[107] where 15% of the genome of the parental strain (E. coli K-12 MG1655) were removed to aid in molecular biology efficiency, removing IS elements, pseudogenes and phages, resulting in better maintenance of plasmid-encoded toxic genes, which are often inactivated by transposons.[108][109][110] Biochemistry and replication machinery were not altered.

By evaluating the possible combination of nanotechnologies with landscape ecology, complex habitat landscapes can be generated with details at the nanoscale.[111] On such synthetic ecosystems, evolutionary experiments with *E. coli* have been performed to study the spatial biophysics of adaptation in an island biogeography on-chip.

Studies are also being performed attempting to program *E. coli* to solve complicated mathematics problems, such as the Hamiltonian path problem.[112]

In other studies, non-pathogenic *E. coli* has been used as a model microorganism towards understanding the effects of simulated microgravity (on Earth) on the same.[113][114]

History

In 1885, the German-Austrian pediatrician Theodor Escherich discovered this organism in the feces of healthy individuals. He called it *Bacterium coli commune* because it is found in the colon. Early classifications of prokaryotes placed these in a handful of genera based on their shape and motility (at that time Ernst Haeckel's classification of bacteria in the kingdom Monera was in place).[85][115][116]

Bacterium coli was the type species of the now invalid genus *Bacterium* when it was revealed that the former type species ("*Bacterium triloculare*") was missing.[117] Following a revision of *Bacterium*, it was reclassified as *Bacillus coli* by Migula in 1895[118] and later reclassified in the newly created genus *Escherichia*, named after its original discoverer.[119]

In 1996 the world's worst outbreak of *E. coli* food poisoning occurred in Wishaw, Scotland, killing 21 people.[120]

See also

- Bacteriological water analysis
- Carbon monoxide-releasing molecules
- Contamination control
- Dam dcm strain
- Eijkman test
- Fecal coliform
- International Code of Nomenclature of Bacteria
- List of strains of *Escherichia coli*
- Mannan oligosaccharide-based nutritional supplements
- Overflow metabolism
- T4 rII system

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Databases and external links

- EcoCyc – literature-based curation of the entire genome, and of transcriptional regulation, transporters, and metabolic pathways
- Membranome database provides information about single-pass transmembrane proteins from E.coli and several other organisms
- *E. coli* statistics (http://redpoll.pharmacy.ualberta.ca/CCDB/cgi-bin/STAT_NEW.cgi)
- *E. coli* Infection | Causes & Risk Factors (http://familydoctor.org/familydoctor/en/diseases-conditions/ecoli-infection/causes-risk-factors.html)
- Bacteriome (http://www.compsysbio.org/bacteriome/) *E. coli* interaction database
- EcoGene (https://web.archive.org/web/20180523221348/http://www.ecogene.org/) (genome database and website dedicated to Escherichia coli K-12 substrain MG1655)
- EcoSal (https://web.archive.org/web/20131011071918/http://ecosal.org/) Continually updated Web resource based on the classic ASM Press publication *Escherichia coli and Salmonella: Cellular and Molecular Biology*
- ECODAB (https://web.archive.org/web/20140609195946/http://www.casper.organ.su.se/ECODAB/) The structure of the O-antigens that form the basis of the serological classification of *E. coli*
- Coli Genetic Stock Center (http://cgsc.biology.yale.edu/index.php) Strains and genetic information on *E. coli* K-12
- PortEco (formerly EcoliHub) (http://porteco.org) – NIH-funded comprehensive data resource for *E. coli* K-12 and its phage, plasmids, and mobile genetic elements
- EcoliWiki (http://ecoliwiki.net) is the community annotation component of PortEco (http://porteco.org)
- RegulonDB (http://regulondb.ccg.unam.mx/index.jsp) RegulonDB is a model of the complex regulation of transcription initiation or regulatory network of the cell *E. coli* K-12.
- Uropathogenic Escherichia coli (UPEC) (http://www.genome.wisc.edu/sequencing/upec.htm)

- AlignACE (http://arep.med.harvard.edu/ecoli_matrices/) Matrices that search for additional binding sites in the *E. coli* genomic sequence

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